Applied Animal Behaviour Science xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

The effects of mining machinery noise of different frequencies on the behaviour, faecal corticosterone and tissue morphology of wild mice (*Mus musculus*)

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ARTICLE INFO

Keywords:
Anthropogenic noise
Circling
Low frequency
High frequency
Mining
Stress

ABSTRACT

Mining noise has a wide variety of frequency spectra and is a potential source of stress for wildlife. We evaluated the effects of mining machinery noise on behaviour and associated physiological parameters at two isoenergetic frequency ranges: high (> 2 kHz) and low (≤ 2 kHz), the latter being less audible to mice, our model species. Effects of these two frequency spectra on behaviour, organ morphology and faecal corticosterone of wild mice were compared with a control treatment with no extra auditory stimuli. The mice exposed to high frequency noise spent less time in their nest than those exposed to low frequency noise or those in the control treatment, and they spent more time circling, especially anticlockwise, which in conjunction with elevated faecal corticosterone levels may reflect a greater right brain hemisphere stress-related response, particularly in females. Low frequency mining noise reduced grooming and circling, suggesting decreased physiological arousal due to mild stress. Low frequencies were also associated with increased faecal corticosterone in males compared to controls, which may be related to gender-based differences of the ear canal that affect frequency sensitivity. In conclusion, high frequency and low frequency mining machinery noise produced stress-related responses that may be important for the animals' welfare and survival.

1. Introduction

Anthropogenic noise is a source of stress for wildlife (Blickley and Patricelli, 2010; Wright et al., 2007). It can disturb acoustic communication, reproduction, community dynamics and behaviour (Blickley and Patricelli, 2010; Rabin et al., 2003; Wright et al., 2007). Chronic exposure to anthropogenic noise can decrease fitness by the repeated activation of the stress response (Romero and Butler, 2007). Noise exposure experiments on captive animals and humans have demonstrated negative effects on immunosuppression and reproductive function; these effects have been suggested as a possible outcome for animals living in the wild (Kight and Swaddle, 2011). Noise exposure also modifies captive animals' emotional state, generating anxiety and depression in rats (Naqvi et al., 2012) and increases in urinary corticoids, locomotion, distress vocalizations and escape attempts in pandas (Owen et al., 2004).

Stereotypic behaviour (i.e. repetitive behaviours induced by frustration, repeated attempts to cope, and/or central nervous system dysfunction, Mason and Rushen, 2008) has been related to noise exposure in primates (Patterson-Kane and Farnworth, 2006), rodents (Anthony et al., 1959) and pandas (Powell et al., 2006). Anthropogenic noise, especially from transportation, has been most studied in relation to its effects on birds and amphibians (Barber et al., 2010; Shannon et al., 2015). It typically has most of its energy output below 2 kHz (Barber et al., 2011; Roberts and Roberts 2009; Slabbekoorn and Peet, 2003). Other acoustic inputs with noxious potential, such as mining noise, have rarely been considered. However, open-cast mining machinery noise has been recognized as potentially dangerous for bats (Armstrong, 2010) and affecting birds' community dynamics (Read, 2000) in similar ways to related industries (rock crushing) (Saha and Padhy, 2011). Open-cast mining and rock crushing machinery produce predominantly low frequency sound waves (Barber et al., 2011; Roberts and Roberts 2009; Slabbekoorn and Peet, 2003). Most commonly used equipment also produces low frequency sound, e.g. dumper trucks and cooling fans from bulldozers whose output is 0.25–0.5 kHz and 0.3–3.5 kHz, respectively (Vardhan et al., 2004; Vardhan et al., 2005). However, rock cutting drills produce dominant frequencies between 2 and 4 kHz (Pal et al., 2006), resulting in a broad spectrum of

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http://dx.doi.org/10.1016/j.applanim.2017.08.008
Received 29 August 2016; Received in revised form 9 August 2017; Accepted 21 August 2017

frequencies at the workface of coal mining sites (0.32 kHz to 8 kHz), but most in the mid to high range (Peng et al., 2010).

On site, mining noise can exceed amplitudes of 90 dB (A) and even reach 110 dB (A) (Ahmad et al., 2014; Utley, 1980). In surrounding areas the amplitude of noise from mining and related industries can exceed 80 dB (A), with small reductions in sound intensity as a result of limited acoustic input attenuating obstructions near the mining site (Mohapatra and Goswami, 2012; Saha and Padhy, 2011). Thus, mining machinery noise is likely to be perceived by a wide arrange of wildlife species, as a result of the broad frequency range and high energy intensity.

One of the animals commonly found in the vicinity of mining sites, due its opportunistic nature, is the mouse, (*Mus musculus*) (Fox and Fox, 2006; León et al., 2007). Its hearing range, from 2 to 92 kHz (measured at 60 dB Sound Pressure Level, SPL) (Heffner and Masterton, 1980; Heffner and Heffner, 2007), would allow it to perceive the mining machinery high frequency components as sound. Although the mouse is acoustically unresponsive to frequencies between 1–2 kHz (at 70–80 dB SPL, Heffner and Masterton, 1980), rodents can experience immunosuppression when exposed to inaudible low frequencies, as can humans in such situations (Aguas et al., 1999a, 1999b; Alves-Pereira and Castelo Branco, 2007).

Although no research exists that compares the effects of different frequencies of anthropogenic noise in mice, it is expected that both low and high frequency mining noise could potentially have negative effects on the behaviour and welfare of this species.

Stress is known to produce variations in rodent behaviours. Hiding, for instance, may increase as a response to threat (Hugie, 2003) and in females, nesting increases as it favors their security and that of their offspring (Taylor et al., 2000). Freezing is a behavioural response to fear and a reaction to perceived threats without a chance to escape (Blanchard et al., 1998; Blanchard et al., 2001). Likewise, maintenance behaviours such as eating and feeding can be effectively suppressed when rodents face environmental stressors (Morley and Levine, 1982; Aguilera et al., 1995).

One behaviour that has already been related to noise exposure in rodents is circling. Circling is an active motion of animals in a circular direction and is considered a stereotypy (Löscher 2010; Pycock 1980). Stress can increase circling behaviour due the actions of glucocorticoids on dopamine release, as glucocorticoids increase the secretion of enkephalines and tachykinines (Reiner and Anderson, 1990), which, in turn, increase nigrostriatal dopamine and locomotion (Biggio et al., 1978; Baruch et al., 1988). Furthermore, the direction of rotational behaviours is determined by hemispheric differences in dopaminergic activity, since animals will turn to the side opposite to the hemisphere with greater dopaminergic action (Carlson and Glick 1996; Ishiguro et al., 2007; Löscher 2010; Schirmer et al., 2007).

Circling behaviour has been observed before during exposure of rats to noise (Lukkes et al., 2009). As the right hemisphere of the brain is typically related to the activation of the stress response (a lateralized brain function, Rogers, 2010), exposure to mining noise could potentially increase this kind of stereotypy in mice. These behavioural responses can also be affected by the hearing sensitivity of animals at different frequencies.

Therefore, in this experiment, the effects of mining machinery noise at two frequency ranges were compared with a control group in a laboratory colony of 'wild mice'. Wild mice in this instance were mice that had not intentionally been genetically modified for laboratory purposes, and which came in our case from the 10th generation of wild-caught animals bred in captivity. We hypothesized that mining noise would disrupt wild mice behaviours, specifically those which are known in rodents to be disturbed by environmental stressors, such as social play (Vanderschuren et al., 1995), grooming (Ducottet and Belzung, 2004) and relevant stereotypies, such as circling (Löscher, 2010; Pycock, 1980). As well as behaviour, we hypothesized that the mining noise would affect physiological parameters associated with stress, in particular faecal corticosterone and the size of immune organs (Zheng et al., 1997; Harper and Austad, 2000). We further hypothesized that the extent of these effects would vary with frequency of the sound.

2. Materials and methods

Procedures were approved by The University of Queensland's Animal Ethics Committee (UQAEC Research Approval Number CAWE/054/13; UQAEC colony approval number SAS/071/10/BREED (NF))

2.1. Study animals

Fifty-seven (34 females and 23 males) wild mice (*Mus musculus*) held at the University of Queensland (UQ) were utilized for the study. The UQ wild mice were originally captured in Darling Downs, Queensland, Australia during June 2004. The colony was originally composed of 16 males and 28 females in 7 litters, arranged on 12 triads (one male with two females). Females from the same litter were kept together to avoid aggression, which had been observed when animals from different litters were housed together. When animals were selected for this study, the colony was in its tenth generation. It had been kept as outbred as possible, making sure that closely related animals did not breed and that the animals still displayed the temperament and behaviour of wild mice. When animals were chosen for breeding there was no selection for any particular trait, to avoid inbreeding problems.

Sample size and sex ratios were established using a similar study previously performed by this group (Mancera, 2016) and was limited by the availability of individuals sourced from student handling practicals at our university. This methodology was chosen in order to follow the 3Rs principles for animal-based experimentation, and only animals that would have been otherwise euthanased were utilized in the study (Understanding Animal Welfare, 2014). All animals were born between 9 and 24 February 2013. Mice were weaned at 4 weeks and they were separated into single- and paired-housing at 4 months old, one week before the beginning of the experiment.

2.2. Diet and animal housing

Mice were fed Rat and Mouse Pellets (Specialty Feeds, Glen Forrest, Western Australia) *ad libitum*. Males were necessarily individually caged because of the risk of aggression, but females were able to be caged in pairs. Both were kept in conventional yellow plastic cages with metallic grid lids on top (females 40 × 24, x 14 cm high, males 31 × 14, x 12 cm high. A 12:12 light:dark cycle provided artificial lighting from 06:00 to 18:00 h, with a temperature range of 21–25 °C. Each cage was supplied with bedding (Sanichip, PJ Murphy Forest Products, USA), plastic tubes for hiding and nesting (2 cm diameter, 10 cm long; two for females and one for males), as well as shredded paper to provide enrichment and nesting material. Bedding and shredded paper were changed twice a week, during the faecal sampling to avoid disturbing the animals. Cages and enrichment tubes were changed for clean ones once weekly. Food and water were checked daily and more provided when needed.

2.3. Experimental treatments and generation of simulated mining noise

Based on the characteristics of mining noise and surface rock crushing (Pathak et al., 1999; Roy and Adhikari, 2007; Saha and Padhy, 2011; Scott et al., 2010) in a fly-in, fly-out (FIFO) mining system (typically operating 24 h, 7 days a week in Australia, (Perry and Rowe 2015) and in consultation with Dr. D. Bridgeman, Senior Director of Geological Services of Manning Mining, Australia, recordings of seven pieces of mining machinery were chosen to recreate the soundscape of open-cast mining facilities: coal truck, drill, bulldozer, shovel, dumper, rock crusher and dragline. A blast was added in order to recreate sound impact from the explosions that occur on mining sites. Specialized

sound effect sources and on-field recordings were used to select the best acoustic samples of machinery (sources list: Supplementary material, Table A). Once acquired, noise samples from individual machinery were mixed and overlapped using appropriate software (Audacity: http://audacity.sourceforge.net/). This process generated seven mining noise soundtracks (combinations and durations of soundtracks: Supplementary material, Table B), which were intended to exemplify open-cast mining. Once generated, the seven soundtracks were individually processed using the high-pass and low-pass filter functions of Audacity software to generate two new tracks per soundtrack: low frequency (LF, ≤ 2 kHz), and high frequency (HF, > 2 kHz). The amplify function was used to generate similar levels of output energy in high and low frequency tracks (spectrograms of the soundtrack 'Coal Truck, Drill and Bulldozer' and the LF and HF tracks generated from this soundtrack; Fig. 1 in Supplementary material). During the playing of the soundtracks in the experiment, the correspondent seven sections were shuffled using appropriate software (Windows Media Player, 2009), in order to avoid habituation to a specific pattern. The blast sequence was played at a random time once a week, consistent with the normal blasting schedule on open-cast mining sites. Since mining and related noises have been only studied as a work hazard for human health, and amplitude has previously been measured as A-weighted decibels which take into account human sensitivity to certain frequencies (Möser, 2009), we used the same amplitude scale to be consistent with previous literature.

After one week of habituation to the experimental rooms and procedures (daily faecal sampling and animal handling, daily amplitude checking and normal animal husbandry), mice were continuously exposed (24 h, 7 days a week) for three weeks to one of the following treatments: Control (C), 12 females and 8 males exposed to no extra auditory stimulation, apart from the normal sounds of daily laboratory activities below 55 dB (mean 54.34 ± 0.45 dB (A)); HF treatment, 10 females and 7 males exposed continuously to the HF tracks; LF treatment, 12 females and 8 males exposed continuously to the LF tracks. HF and LF treatments had a range of mining noise amplitude of 70–75 dB (A) (HF mean value = 72.93 ± 1.01 dB (A); LF mean value = 71.50 ± 0.79 dB (A)). Mean values for amplitude ranges were calculated using recordings taken in the high frequency, low frequency and control rooms while the noise was being broadcasted. Then, decibel values were extracted from the recordings in successive samples using the function 'Sample Data Export' from the software Audacity® (an increase of 10 dB is an increase in noise power by a factor of 10, Goelzer et al., 2001). All amplitude levels were measured daily with a sound level meter (Digital Sound Level Meter, Q1362, Dick Smith Electronics).

Our amplitude range was known to activate the stress response in wild mice (Mancera, 2016), and it approximated the energy reported 500–1000 m from stone mining and crushing operations (Saha and Padhy, 2011), and in residential and commercial areas adjacent to mining facilities, which had recorded amplitudes of 67and 89 dB (A), respectively (Mohapatra and Goswami, 2012).

To minimise substrate vibrations generated by the noise soundtracks, we placed the speakers on surfaces separated from those where the cages were positioned, thus preventing physical contact at any point. Likewise, the floor in the rooms was made of thick solid concrete, which is a material recognized for its noise dampening properties (Long 2005) and a close to zero sound absorption coefficient (http://www.acousticalsurfaces.com/acoustic_IOI/101_13.htm), which makes it a good material to avoid substrate vibrations.

2.4. Experimental enclosures

The study took place at the Queensland Animal Science Precinct (QASP) in the University of Queensland, Gatton, Australia. A hexagonal facility with six identical rooms was used to separate the animals into three treatment rooms, each separated from the next by an empty room. Rooms containing mouse treatments were soundproofed using noise and temperature-isolating materials (Reflecta, GID Double Layer, Insulation for sale, NSW, Australia), as well as soundproofing foam (Broadband Studio Acoustic Foam, Swamp Industries Pty Ltd, NSW, Australia) as necessary. Animals were placed in their cages at distances of 80–266 cm from the speakers (System Frequency response: 35 Hz-20 KHz, Output Power (Total) 200 W, Speaker system z623, Logitech, Switzerland) (room, cages and speakers setting: Figure II, Supplementary material). Noise decibels in treatment rooms were measured daily at the furthest and the nearest cages from the speaker, using the sound level meter previously mentioned. Our measures showed a maximum decibel difference of ± 0.5 dB between the cages positioned at 266 cm compared to those set at 80 cm. Because of this small volume difference, noise amplitude was always in the 70–75 dB (A) range for all cages in Treatments LF and HF. There was no difference between the noise decibel levels between cages at different ends of the control room.

2.5. Video recordings and analysis of videos

Mice behaviour was recorded by 12 surveillance cameras (1 camera/2-4 cages) (model K-32HCF, Kobi CCD, Ashmore, Australia) suspended 60 cm above the cages and connected to a video recorder (Model Lite 900, LG, Yeouido, South Korea). Researchers were present in the experimental rooms between 9:00 to 11:00 h for cleaning duties and collection of faecal samples. Animals were videorecorded continuously throughout the experimental period. A stratified model was designed for behavioural analysis, in which randomly distributed experimental days were selected equally from these blocks. From the videos gathered during the experiment, 12 representative days in three blocks were selected for analysis (block 1: days 3, 4, 5, 6; block 2: days 12, 13, 19, 20; block 3: days 25, 26, 27, 28 (the last days of noise exposure)). Blast days within the observation blocks were days 3, 13 and 27 of the experiment. Days for blocks were selected to represent the start, mid-point and end of the study. Blocks were composed of consecutive days, with the exception of block 2, which was composed of 2 days at the beginning and end of the mid-section of the experiment due to unexpected loss of video records before analysis. Due to video loss, 71.5% of the selected videos were successfully analyzed. On each day, a period of six hours (one quarter of the day) was observed per animal, without repeating the same quarter twice, adding up to a total of 24 h/animal/block. Within each period, behaviours were recorded for the first 5 min of each hour using the continuous focal observation method (Martin and Bateson, 1993) (visual representation of the observational model: Table C, Supplementary material).

Taking into account behaviours that are associated with stress in mice (Denmark et al., 2010; Grant and Mackintosh, 1963; McAllister and Dixon, 1989; Sluyter et al., 1995; Van de Weerd et al., 1998; Van Oortmerssen 1971) and the behaviours observed for this colony during the experimental set-up, ethograms to assess stress-related behaviours were created to separately measure individual behaviour of all mice, and social behaviour for female pairs. The behaviours chosen have been previously reported to vary in frequency and duration during environmental stress exposure, therefore making its assessment relevant to evaluate the effects of mining noise frequencies (relations between behaviours and literature specifying their relation with stress are included in Table D, Supplementary material). The individual behaviours recorded were full body hiding (inside the tube), partial hiding (leaving the head outside the tube), mouse active or inactive inside a nest, determined by movement of a shredded paper nest or the tube when it was used for nesting, nest building (activities related to constructing of the nest, such as gathering and rearranging of paper), drinking, feeding, freezing (mouse remaining still in one position, with the only detectable movement being breathing), grooming self, moving on the grid (moving upside down on the bars of the metallic grid lid, but not circling) and circling anticlockwise or clockwise (locomotion on the metallic grid lid or on the cage floor in an anticlockwise or clockwise direction from a

mouse perspective).

Social behaviours recorded were pushing under another (one mouse moves under the other led by their snout), sniffing each other's snout, sniffing each other's anal area, chasing (one animal pursuing the other), allogrooming, mounting (one mouse moves on top of the other either in a copulation-like manner or aligning snout to tail), being inactive socially but in close proximity (mice remain engaged in individual behaviours while touching each other or remaining within one body width), touch and go (one individual touches its partner briefly and runs away), squire (walking while follower keeps its snout close to the leader's anal area) and push away (one mouse pushes the other in an aggressive manner, i.e., displacing the subject). Due the unexpected loss of video recordings referred to above, only 82.8% of social behaviour was successfully analyzed.

During replay, the duration and rates of these behaviours were recorded using the software 'Cowlog' (Hänninen and Pastell, 2009). In order to record rates and start points of durations, a change of behavioural state was determined by an animal spending at least 3 s performing a new behaviour. This system was based on preliminary observations of the videos from this experiment and taking into account standard systems for measuring behaviours (Martin and Bateson, 1993).

2.6. Faecal sampling and processing

Samples were collected daily between 9:00 to 11:00 h by removing mice from their cages using the tubes as containers in order to avoid direct handling. Fresh faeces from pairs of females or solitary males were sampled within approximately 20 h, taking into account moisture content and color (often the handling process stimulated animals to defecate, which allowed the collection of fresh faecal material). We aimed to collect approximately 5 g faecal matter each time, thus collecting both recently excreted faeces (if present) and all the fresh material present inside the cage. After collection, faeces were collected in a cooler with ice packs as recommended by Wielebnowski and Watters (2007), where they remained for not more than 2 h. Later, the samples were frozen at −80 °C to prevent degradation, as recommended by Touma et al. (2004). Once all samples had been collected, faecal samples from periods of 4 consecutive days were pooled, generating 7 pooled samples per replicate. Samples were then freeze-dried for 5 h, homogenized with a mortar, weighed (to the nearest 0.05 ± 0.0015 g) into glass scintillation vials and 1 ml of 80% methanol was added. They were then centrifuged at 800*g* for 10 min and the extract decanted and frozen at −20 °C.

The concentration of faecal corticosterone metabolites (FCM) was determined by a corticosterone enzyme immunoassay (EIA) technique described previously, but with minor modifications (Keeley et al., 2012). Microtitre plates pre-coated with goat anti-rabbit globulin (Arbor Assays, USA; A009) were used for this purpose, and corticosterone antibody (stock dilution: 1:200) and horse-radish peroxidase (stock dilution: 1:200) (C Munro, UC Davis, CA, USA) at 1:120,000 and 1: 250,000 dilution rates, respectively, 100 µl per well. Faecal samples were diluted in assay buffer prior to analysis (1:7 for females, 1:6 for males) and a serial dilution of a pool of randomly-selected faecal samples demonstrated parallelism with the standard curve. The intra- and inter-assay coefficients of variation were 2.65% and 7.09%, respectively. Cross-reactivities for the corticosterone EIA antibody were corticosterone 100%, deoxycorticosterone 14.3%, tetrahydrocorticosterone 0.9%, cortisol 0.2%, progesterone 2.7%, testosterone 0.6% and < 1% for all other steroids tested. The sample color absorbance values were determined using a microplate spectrophotometer reader (Epoch, Winooski, VT, USA) and appropriate software (Gen 5, Biotek, USA). Test and reference filters were 405 and 630 nm, respectively.

2.7. Tissue collection, processing and evaluation

As part of the normal end-of-year procedures to avoid a surplus of animals in this teaching colony, animals were euthanized by cervical dislocation, immediately followed by assessment of total body weight and the dissection and weighing of spleen, adrenal gland and thymus. Afterwards, organs were preserved in a 10% neutral buffered formalin solution. Subsequently, tissue slides were generated by routine paraffin embedding, 4 µm sectioning and staining them with haematoxylin and eosin (H & E). Using a binocular microscope (Eclipse Ci Microscope, Nikon Instruments Inc, Tokyo, Japan), and Nikon Nis Elements Basic Research (Nikon Instruments Inc, Tokyo, Japan) software, the adrenal cortex and medulla thicknesses (in µm) were determined, and cortex/medulla ratios calculated. Spleen thickness was measured using the same technique. To estimate white matter percentages in the spleen, one region was randomly chosen and the total area measured by the software after manual outlining (μm^2). Afterwards, white matter within the selected area was visually identified by a trained observer, outlined and measured by the software. Percentages of white matter were calculated by contrasting with the total area selected.

2.8. Statistical analysis

In order to analyze individual and social behaviour and to eliminate left side skewness of the data due to inflated zeros, a preliminary analysis was performed to compare inactivity between time quarters using a Linear Effects Mixed Model (LEM) with the fixed factors quarter, block, sex, treatment, quarter*block, quarter*sex, quarter*-treatment, block*sex, block*treatment, sex*treatment and random factor cage (treatment*sex). F-values for this LEM models are approximated using the Kenward-Roger procedure, thus obtaining non-integer values for the denominator degrees of freedom as a standard SPSS procedure. The duration of nest inactivity was squared to generate residuals that were normally distributed using The Shapiro–Wilk test. ($P \geq 0.05$). Mean inactivity was significantly different between quarters ($F_{3,291.75} = 20.83$; $P < 0.0001$). From the total time analyzed in a given quarter (5 min * 6 h = 30 min), quarters 3 and 4 (0500 to 1000 h and 1100 to1600 h, respectively, each of 6 h, were the periods with more inactivity (73.3 ± 16.8% and 73.9 ± 16.9% of inactive time, respectively), whereas quarters 1 and 2 (1700–2200 h and 2300–400 h, respectively) were the most active (53.1 ± 24.2% and 61.7 ± 16.6% of inactive time, respectively) ($F_{3,291.88} = 20.83$; P value for differences between 1/2 and 3/4 < 0.0001). Based on this analysis, quarters 1 and 2 were aggregated to analyze individual behaviour variables, eliminating the factor quarter for further analysis, as quarters 1 and 2 represent a continuous 12 h period. Calculations were performed with the program IBM SPSS statistics, version 20.

Following this, a LEM was used which included the factors mouse, treatment, sex, and block. F-values for this LEM models are approximated using the Kenward-Roger procedure, thus obtaining non-integer values for the denominator degrees of freedom as a standard SPSS procedure. Residuals were tested for normal distribution using the Shapiro–Wilk test, and if not normally distributed ($P < 0.05$) data was transformed using square root, logarithm_{10} or inverse transformation ($1/(x + 1)$), whichever most effectively returned residuals to a normal distribution. Failing this, variables were analyzed using the Kruskall–Wallis test, and, if significant ($P < 0.05$), Mann–Whitney *U* tests with Bonferroni correction for multiple comparisons were used to contrast mean ranks. To observe individual females caged in pairs, during video replay one mouse was initially selected for behaviour recording by the observer, then the video was replayed and the behaviour of the remaining mouse was recorded. Rates and durations of behaviours for pairs of females were analysed as means per cage. For social behaviors, data from all quarters was transformed to binomial values and tested by a Binary Logistic Regression (BLR) model that included the factors treatment, block, and cage number. With this

model, the presence and absence of behaviours between treatments were compared.

Faecal corticosterone was analyzed using a LEM, including the factors mouse, treatment, sex and period of time. F-values for this LEM models are approximated using the Kenward-Roger procedure, thus obtaining non-integer values for the denominator degrees of freedom as a standard SPSS procedure. Data was transformed using logarithm$_{10}$, to return residuals to a normal distribution ($P < 0.05$). When LEM was significant, a post-hoc analysis with Bonferroni corrections was used to compare means. Results were considered significant at $P \leq 0.05$.

Tissue morphology and organ weight were analyzed using General Linear Models (GLM). Tissue and organ variables included the factors sex and treatment with body weight as a covariate, and faecal corticosterone included sex, treatment and period of time. Residuals were tested for normal distribution as above, and if not normally distributed ($P < 0.05$) data was transformed using square root or logarithm$_{10}$, whichever most effectively returned residuals to a normal distribution.

Due to the chances of Type I errors while performing multiple comparisons, we used a "false discovery rate" correction procedure (FDR) (Benjamini and Hochberg, 1995) with a Q value = 0.1 to strengthen statistical significance. This procedure was performed in seven different groups of the P values obtained, which were sorted by the statistical test used (LEM, GLM or KW), and the independent variable contrasted (treatment, sex or treatment*sex).

All calculations were performed with Minitab Statistical Software, version 16, or IBM SPSS statistics, version 20. Results were considered significant at $P \leq 0.05$.

3. Results

3.1. Effects of mining noise on behavior

The time spent in, and number of bouts of, partial hiding were less in HF than LF ($P = 0.02$) (Tables 2 and 4). HF mice also spent considerably less time active and had fewer bouts inside the nest compared to LF and C ($P = 0.02$ and 0.04, respectively) (Tables 1 and 3). C mice had fewer bouts of inactivity in the nest than mice in LF ($P = 0.03$, Table 3) and they had more bouts of climbing than mice in LF or HF ($P = 0.004$) (Table 3). Mice exposed to LF groomed themselves less than those in C and HF ($P = 0.04$) (Table 1).

Animals exposed to HF ($P < 0.0001$) and C ($P = 0.01$) treatments spent much more time circling anticlockwise than those in LF (Table 2), and HF mice had more bouts of circling anticlockwise than LF ($P < 0.0001$) (Table 4). The total time spent circling was higher for mice in HF than for mice in LF ($P = 0.03$, Table 2), and there were more circling bouts in HF mice than LF mice ($P = 0.04$, Table 4).

In social behaviour, there were no significant differences when presence and absence of behaviours were analyzed (Table E, Supplementary material).

3.2. Faecal corticosterone metabolites (FCM)

Overall, mice in treatment HF tended to have increased FCM compared with C and LF, and females had higher levels than males ($P < 0.0001$) (Table 1). In addition, in females exposed to HF, FCM were increased compared with those in LF and C, and in males FCM were reduced in C males compared with those in LF and HF treatments ($F_{2,239.56} = 19.383$; $P < 0.0001$; treatment* sex interactions compared with post-hoc Bonferroni test are displayed with letter superscripts in Table 1)

3.3. Organ weights and morphology

Females were lighter than males (mean body weight female: 17.9 g, male 22.8 g, $P < 0.001$) (Table 5) and they had a thicker adrenal cortex and higher cortex/medulla ratio (Table 6).

4. Discussion

We found in a previous experiment that mining noise at 70–75 dB (A) generated detrimental effects on behaviour, organ size and morphology (Mancera, 2016). In this respect, this experiment showed that noise at this amplitude applied at different frequency ranges had strong behavioural and physiological effects.

4.1. Behavioural and physiological effects of high frequency mining noise

HF noise changed mice behavior, with less time performing activities inside the nest compared to LF and C. Mice calls above 2 kHz are important for survival, as wriggling calls of between 2 and 10 kHz are emitted by pups to seek attention and stimulate parental care (Ehret, 2013; Ehret and Bernecker, 1986). Distress calls (2–30 kHz at 80–90 dB) and defensive calls from females (2–100 kHz at 80 dB) which are produced by adults outside the maternal context have similar characteristics (Ehret, 2013) and are also associated with locomotion and exploration. It is likely that some acoustic components of our HF treatment were similar to those calls, increasing activity outside the nest due to exploration and reducing time inside the nest. Similar effects have been reported for the Stephen's Kangaroo rat (*Dipodomys stephensi*), which elicits foot-drumming, a behaviour reserved for territorial and mating purposes, when exposed to traffic noise (Shier et al., 2012). The acoustic processing of anthropogenic acoustic signals by

Table 1
Durations of individual behaviours and faecal corticosterone concentrations of mice exposed to mining noise at different frequencies contrasted by treatment. HF = High frequency treatment, LF = Low frequency treatment, C = Control treatment. SED = Standard Error of the Difference. $F_{NDF,DDF}$ = F value $_{NumeratorDegreesofFreedom,DenominatorDegreesofFreedom}$. Means of faecal corticosterone that do not share a letter are statistically different. There were no significant treatment x sex interactions for behavious ($P < 0.05$).

Hormone/behaviour	Means						SED	$F_{NDF,DDF}$ (P value)
	Females			Males				
	HF	LF	C	HF	LF	C		
Hiding (1/(s/30 min + 1))	0.61	0.39	0.52	0.75	0.66	0.58	0.069	$2.82_{2,160}$ (0.06)
(s/30 min)	0.63	1.52	0.93	0.34	0.53	0.73	–	–
Nest active (√s/30 min)	6.83	14.33	11.84	8.62	11.14	11.54	1.68	$4.74_{2,31.94}$ (0.02)
(s/30 min)	46.58	205.41	140.21	74.34	124.06	133.06	–	–
Nest inactive (s/30 min)	1077.5	984.2	902.7	882.9	1109.7	803.7	88.16	$2.61_{2,32.84}$ (0.09)
Climb (√s/30 min)	12.69	7.47	9.17	8.29	6.55	10.36	1.801	$2.1_{2,32.12}$ (0.03)
(s/30 min)	161.21	55.79	84.03	68.66	42.89	107.33	–	–
Groom (log_{10} s/30 min + 1)	1.38	1.19	1.39	1.39	0.86	1.63	0.189	$3.71_{2,34.27}$ (0.04)
(s/30 min)	23.04	14.74	23.89	23.27	6.16	41.46	–	–
Faecal corticosterone (log_{10} ng/ml)	2.58^{a}	2.40^{b}	2.42^{b}	2.40^{b}	2.39^{b}	2.32^{c}	0.013	$42.43_{2,239.34}$ (< 0.0001)
(ng/ml)	385.5	254.7	261.2	252.9	247.2	212.3	–	–

Table 2
Durations of individual behaviours of mice exposed to mining noise at different frequencies contrasted with Kruskal-Wallis test ($_{KW}$). Ranks were contrasted using the Mann-Whitney test ($_{MW}$) with Bonferroni correction. HF = High frequency treatment, LF = Low frequency treatment, C = Control treatment. χ^2_{DF} = Chi squared value $_{DegreesofFreedom}$. P_{KW} = P value for the Kruskal-Wallis test P_{MW} = P value for the Mann-Whitney test.

Behaviour	Mean rank					χ^2_{DF} (P_{KW}) Treatments	Z (P_{MW}) HF vs C	Z (P_{MW}) HF vs LF	Z (P_{MW}) LF vs C
	HF	LF	C	Females	Males				
Partial hiding, rank	77.6	92.5	90.7	91.6	84.2	8.18_2 (0.02)	−2.34 (0.06)	2.66 (0.02)	0.73 (1.00)
Nest building	96.3	79.2	88.4	95.2	81.3	3.2_2 (0.2)	–	–	–
Drink	96.3	78.4	88.4	94.7	81.6	3.4_2 (0.2)	–	–	–
Feed	95.9	78.4	89.6	93.7	82.4	3.6_2 (0.2)	–	–	–
Freeze	91.1	91.8	80.3	90.1	85.4	4.1_2 (0.1)	–	–	–
Circle anticlockwise	101.3	71.1	92.3	98.2	78.8	15.9_2 (< 0.00001)	1.15 (0.8)	-3.83 (< 0.0001)	−2.82 (0.01)
Circle clockwise	89.1	88.4	85.4	92.6	83.4	0.3_2 (0.8)	–	–	–
Total Circling	96.6	74.9	92.3	99.8	77.5	7.6_2 (0.02)	0.501 (1.00)	−2.54 (0.03)	−2.14 (0.09)

wild animals and its influence on their behaviour may produce both confusion over the interpretation of threats in their environment and unwanted energy expenditure.

Female mice exposed to HF had the highest levels of FCM, compared to those in C and LF exposure. Likewise, HF males had increased levels compared to C males. Mouse hearing range is typically from 2.3 to 92 kHz at 60 dB SPL (Heffner and Masterton, 1980; Heffner and Heffner, 2007) and they are acoustically poorly responsive to frequencies between 1 and 2 kHz at 70–80 dB SPL (Heffner and Masterton, 1980). Thus, the HF treatment was probably audible for all mice, which made the high frequency mining noise more likely to produce the known behavioural and physiological stress responses related to acoustic perception of noise.

As HF females showed the highest levels of FCM compared with other females and males in all treatments, gender may play an important factor in frequency susceptibility. Sex- steroid hormones, in particular oestrogen, modulate auditory processing and influence frequency perception (Caras, 2013). Human females have better sensitivity for high frequency sounds than males (Chung et al., 1983) and have developed a better auditory sensitivity to detect threats (Caras, 2013), whereas males perform better auditory tasks related to spatial orientation for navigation (Clint et al., 2012). In female mice, oestrogen released episodically through the oestrous cycle increases behavioural responses to synthetic and recorded pup wriggling calls (Ehret and Schmid, 2009). As these calls are between 2 and 10 kHz (Ehret and Bernecker, 1986), it is likely that sensitivity to this frequency range increases is oestrogen mediated. Oestrogen administration to ovariectomized rats accelerates their auditory brainstem responses to sound stimuli (Coleman et al., 1994), which is evidence of increased auditory perception (Hall, 2007). Thus reproductively active female mice may have greater senstivity to HF than males. In addition to the reduction of activity in the nest, mice in the HF treatment spent more time circling, which may reflect a greater stress-related response. Circling is a stereotypy generated by imbalances in dopamine release, whereby animals turn to the side opposite to the hemisphere with greater dopaminergic action (Carlson and Glick, 1996; Ishiguro et al., 2007). Stress stimulates circling behaviour in rodents, as glucocorticoids indirectly increase nigrostriatal dopamine and locomotion (Baruch et al., 1988; Biggio et al., 1978); hence the increased circling could have been a direct consequence of increased glucocorticoid release in the HF treatment.

In addition, mice in the HF treatment also increased anticlockwise circling compared to other treatments. Circling direction is a product of brain lateralization, a central tenet in neuroscience which attributes different functions to the brain hemispheres (Csermely and Regolin, 2012). Whereas the left hemisphere controls the right side of the body and regulates communication, attention, learning and established behaviours, the right hemisphere controls the left side of the body and regulates responses to threatening situations, social interactions and novelty (Ocklenburg and Gunturkun, 2012; Rogers, 2010). Therefore, environmental stress will selectively activate the right hemisphere (Rogers, 2002), influencing dopamine release.

Rats exposed to controllable or uncontrollable electrical foot-shock increased dopamine production in the right prefrontal cortex (Carlson et al., 1993), upregulating nigrostriatal dopamine and anticlockwise circling (Carlson et al., 1987). In this experiment, the increase in left (anticlockwise) circling during HF exposure is probably related to an enhanced stress response mediated by the right brain hemisphere.

4.2. Behavioral and physiological effects of low frequency mining noise

Along with HF exposure, LF noise increased FCM in males compared to C. In chinchillas (McFadden et al., 1999) and humans (Chung et al., 1983), males have slightly increased hearing capabilities at 1–2 kHz compared to females, probably due a larger ear canal size and volume

Table 3
Bouts of individual behaviours of mice exposed to mining noise at different frequencies contrasted by treatment. HF = High frequency treatment, LF = Low frequency treatment, C = Control treatment. SED = Standard Error of the Difference. $F_{NDF,DDF}$ = F value $_{NumeratorDegreesofFreedom,DenominatorDegreesofFreedom}$. There were no significant treatment x sex interactions. ($P < 0.05$).

Hormone/behaviour	Means						SED	$F_{NDF,DDF}$ (P VALUE)
	Females			Males				
	HF	LF	C	HF	LF	C		
Nest active (log_{10} bouts/30 min +1)	0.41	0.71	0.55	0.48	0.54	0.43	0.069	$3.65_{2,33.55}$ (0.04)
(bouts/30 min)	1.55	4.08	2.58	2.01	2.47	1.71	–	–
Nest inactive (bouts/30 min)	4.85	5.23	4.09	4.69	5.47	4.06	0.467	$3.93_{2,34.35}$ (0.03)
Climb (log_{10} bouts/30 min + 1)	0.76	0.54	1.19	0.45	0.46	0.69	0.131	$6.58_{2,35.13}$ (0.04)
(bouts/30 min)	4.81	2.45	14.49	1.81	1.85	3.93	–	–
Feed (bouts/30 min)	1.39	1.21	1.67	1.49	0.99	1.48	0.304	$1.36_{2,30.64}$ (0.3)
Groom (log_{10} bouts/30 min +1)	0.36	0.42	0.39	0.43	0.25	0.48	0.068	$1.29_{2,35.09}$ (0.3)
(bouts/30 min)	1.29	1.63	1.5	1.68	0.76	2.03	–	–

Table 4
Bouts of individual behaviours of mice exposed to mining noise at different frequencies contrasted with Kruskal-Wallis test ($_{KW}$). Ranks were contrasted using the Mann-Whitney test ($_{MW}$) with Bonferroni correction. HF = High frequency treatment, LF = Low frequency treatment, C = Control treatment. χ^2_{DF} = Chi squared value $_{DegreesofFreedom}$. P_{KW} = P value for the Kruskal-Wallis test P_{MW} = P value for the Mann-Whitney test.

Behaviour	Mean rank					χ^2_{DF} (P_{KW}) Treatments	Z (P_{MW}) HF vs C	Z (P_{MW}) HF vs LF	Z (P_{MW}) LF vs C
	HF	LF	C	Females	Males				
Hiding	74.89	93.59	91.88	98.74	78.37	5.01_2 (0.08)	–	–	–
Partial hiding	77.59	92.75	90.48	90.99	84.67	8.25_2 (0.02)	−2.302 (0.06)	2.69 (0.02)	0.43 (1.00)
Nest building	88.41	96.31	78.08	92.13	83.74	4.35_2 (0.1)	–	–	–
Drink	96.30	76.57	91.01	95.10	81.33	5.08_2 (0.08)	–	–	–
Freeze	91.53	91.81	79.94	89.68	85.73	4.53_2 (0.1)	–	–	–
Circle anticlockwise	101.83	71.39	91.56	97.57	79.32	15.8_2 (< 0.0001)	1.31 (0.6)	-3.86 (< 0.0001)	−2.69 (0.02)
Circle clockwise	88.83	88.52	85.40	92.49	83.44	0.32_2 (0.85)	–	–	–
Total circling	97.04	75.78	91.19	98.92	78.22	6.89_2 (0.03)	0.69 (1.00)	−2.49 (0.04)	−1.91 (0.2)

Table 5
Organ weights, corrected for body weight of wild mice exposed to mining noise at different frequencies. F = female, M = male, HA = High noise treatment, LA = Low noise treatment, C = Control treatment, SED = Standard Error of the Difference. $F_{NDF,DDF}$ = F value $_{NumeratorDegreesofFreedom,DenominatorDegreesofFreedom}$.

Organ	Means						SED	$F_{NDF,DDF}$ (P VALUE)		
	Females			Males				Treatments	Sex	Treatment x sex
	HF	LF	C	HF	LF	C				
Total body weight (g)	17.01	18.52	18.18	22.01	23.68	22.68	0.693	$0.83_{2,34}$ (0.45)	$24.14_{1,34}$ (< 0.0001)	$0.04_{2,34}$ (0.9)
Spleen (√g)	0.157	0.178	0.183	0.185	0.178	0.162	0.0057	$0.24_{2,33}$ (0.8)	$0.04_{1,33}$ (0.8)	$2.83_{2,33}$ (0.07)
(g)	0.0246	0.0316	0.334	0.0342	0.0316	0.0262	–	–	–	–
Adrenal glands (√g)	0.116	0.121	0.097	0.156	0.133	0.129	0.0074	$1.22_{2,28}$ (0.31)	$3.34_{1,28}$ (0.08)	$0.61_{2,28}$ (0.55)
(g)	0.0146	0.027	0.0094	0.0176	0.0243	0.0166	–	–	–	–
Thymus (log_{10} g + 1)	0.0129	0.0093	0.0105	0.0804	0.00074	0.0125	0.0016	$0.64_{2,32}$ (0.5)	$0.27_{1,32}$ (0.61)	$0.7_{2,32}$ (0.5)
(g)	0.0301	0.021	0.0244	0.0186	0.0171	0.0292	–	–	–	–

Table 6
Morphological characteristics of adrenal glands and spleen corrected for body weight of wild mice exposed to mining noise at different frequencies contrasted by treatments and sex. F = female, M = male, HA = High noise treatment, LA = Low noise treatment, C = Control treatment, SED = Standard Error of the Difference. $F_{NDF,DDF}$ = F value $_{NumeratorDegreesofFreedom,DenominatorDegreesofFreedom}$.

Tissue property	Means						SED	$F_{NDF,DDF}$ (P VALUE)		
	Females			Males				Treatments	Sex	Treatment x sex
	HF	LF	C	HF	LF	C				
Spleen Thickness (μm)	1238	1075	1265	1441	1374	1408	85.82	$0.46_{2,33}$ (0.6)	$1.54_{1,33}$ (0.2)	$0.17_{2,33}$ (0.8)
White matter (%)	51.17	56.4	45.86	48.36	60.17	56.5	4.069	$0.8_{2,33}$ (0.5)	$0.26_{1,33}$ (0.62)	$0.43_{2,33}$ (0.7)
Adrenal Gland Cortex (μm)	316.7	319.4	304.1	206.2	223.5	191.2	11.446	$0.67_{2,29}$ (0.5)	$23.4_{1,29}$ (< 0.0001)	$0.1_{2,29}$ (0.9)
Medulla (μm)	257.4	312.6	271.4	220.1	278.9	261.1	18.241	$1.38_{2,29}$ (0.3)	$0.6_{1,29}$ (0.45)	$0.09_{2,29}$ (0.9)
Cortex/medulla ratio (√(μm/μm))	1.33	1.051	1.18	0.985	0.809	0.792	0.0591	$2.22_{2,29}$ (0.13)	$8.12_{1,29}$ (0.008)	$0.24_{2,29}$ (0.8)

(Hellström, 1995), thus potentially creating some auditory responsiveness below 2 kHz in this gender.

LF noise produced a decrease in grooming in all mice, which has been observed in mice exposed to combination of unpredictable social and environmental stressors, and hypothesized to be an apathetic reaction to the stress (Ducottet and Belzung, 2004). Similarly, there was also a decrease on circling anticlockwise and total circling in LF when compared to HF and C. In previous experiments performed by our group with unfiltered mining noise of different amplitudes, circling behaviour increased during high amplitude exposure (70–75 dB (A)) as a possible mechanism to inhibit stress (Mancera, 2016). In this experiment, the reduction in circling in observed in LF on this experiment may be compatible with the physiological stress observed through increased FCM in males compared to their controls. Chronic unpredictable mild stress in male rats has increased glucocorticoids and produced an anhedonic decrease in activity in an open field test (Liu et al., 2014). Similarly, repeated unavoidable stress exposure (50 min, one electric shock/30 s) has increased corticosterone and decreased escape attempts in male rats (Raone et al., 2007). Therefore, chronic and unpredictable LF mining noise as a source of mild stress could also have reduced circling and grooming as a result of physiological unresponsiveness, to which males appeared to be more sensitive due to the increased FCM levels. Furthermore, low frequency mining noise increased the time mice spent inactive and hiding, compared to the control and high frequency noise treatments, which can also be an effect of mild stress, physiological unresponsiveness and/or anhedonia.

4.3. Limitations of the study

We recognize that the assessment of the effects of noise stress can be affected by factors such as the position of the cage in terms of the quality of noise exposure. Nonetheless, as described in our methods, we measured amplitude levels experienced in cages positioned at different distances from the speakers, and the dB (A) range was always within

the target values. This suggests that there were no meaningful differences in noise exposure between cages. Other factors that can affect the stress experienced by animals are the visual access to other individuals through clear cages (Cloutier and Newberry, 2010) or cages positioned at different levels (Izidio et al., 2005). Hence we used yellow plastic cages that prevented visual contact between animals in the same room, all positioned at the same height from the floor.

Another factor that could have affected the validity of the results observed in this experiment was the spatial isolation of treatments, as emissions from animals that responded in an extreme way to treatment, e.g. by producing pheromones or alarm calls, could be a cofounding factor for the effects observed, potentially causing pseudoreplication (Hurlbert, 1984; Lazic, 2010). In some studies this possibility can be counteracted through interspersion or intercalating cages of experimental treatments in the same space (Hurlbert, 1984). However, the effects of noise stress must be tested in separate rooms due to technical reasons, as noise exposure techniques do not allow the simultaneous exposure of animals to three types of auditory treatments in the same space.

Another possible source of pseudoreplication for this experiment could have been the distribution of litters within experimental treatments (Lazic, 2010). Nonetheless, the assignment to treatments was randomized and the behavioural and physiological measures on females (which always belonged to the same litter) were averaged, thus mimimizing this possibility (Hurlbert, 1984; Lazic, 2010).

Given these facts, it is important to recognize that although the results obtained on this study are both meaningful and unique, they need to be further replicated taking into account the challenges that this novel methodology presented to measure anthropogenic noise stress.

5. Conclusions

There was a greater responsiveness to high frequency than low frequency mining noise, which probably reflects the audibility of the two frequency spectra. Mice exposed to high frequency noise increased circling and reduced activity in the nest, which in conjunction with increased FCM levels, suggests an elevated stress response, which is more relevant in females. Mice exposed to low frequency noise reduced grooming, and circling, suggesting a decreased physiological arousal due to mild stress. For LF, FCM was increased in male mice compared to their control, which may be due to males' increased responsiveness to low frequencies noise due to ear canal differences related to gender. Therefore, frequencies below and above 2 kHz had differential effects on male and female wild mice that may have important consequences for their welfare and survival.

Acknowledgements

We greatly appreciate the support given by Sonia Fardell, Chief Investigator of the wild mice colony in UQ-Gatton, as well as the personnel of QASP on providing training and materials for the completion of this experiment. The research was funded by the Centre for Animal Welfare and Ethics at the University of Queensland.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2017.08.008.

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